The Diplopod Community of a Mediterranean Oak Forest in Southern France: Ecological and Evolutionary Interest

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ABSTRACT

Seven millipede species have been found in a holm oak forest (*Quercus ilex*) sampled for two years. Seasonal changes in abundance are discussed in relation to the periods of recruitment and the changes in vertical distribution of species. Details of the life cycle of *Opisthocheiron elegans* are given. The biomass of macrosaprophagous species (on average 10.5 g live mass/m^2 for *Glomeris marginata* and *Cylindroiulus caeruleocinctus*) is the highest recorded in Europe, which points to the ecological importance of millipedes in Mediterranean forests. The millipede populations from the site studied differ intraspecifically from those found further north, as shown in *Polyzonium germanicum*. The significance of this geographical variation is discussed.

RÉSUMÉ

Le peuplement de diplopodes d'une forêt de chêne-vert dans le sud de la France.

Le peuplement de diplopodes d'une forêt de chêne vert (*Quercus ilex*) est décrit après deux années d'échantillonnage. Il comprend cinq espèces régulières et deux espèces occasionnelles. Les variations saisonnières d'abondance sont examinées en liaison avec les périodes de recrutement et les variations de la distribution verticale des populations. Quelques données sur le cycle biologique d'*Opisthocheiron elegans* sont présentées. La biomasse des espèces macrosaprophages présentes — en moyenne 10.5 g/m^2 (masse fraîche) pour *Glomeris marginata* et *Cylindroiulus caeruleocinctus* — est la plus élevée de toutes celles mesurées en Europe, ce qui souligne l'importance écologique des diplopodes dans certaines forêts méditerranéennes. Les populations de diplopodes de la station étudiée se différencient intraspécifiquement de celles trouvées plus au nord, comme le montre le cas de *Polyzonium germanicum*. La signification de cette variation géographique est discutée.

INTRODUCTION

The work of JANATI-IDRISSI (1988) on litter consumption in Mediterranean ecosystems drew attention to the millipede community of the forest of Puechabon, Hérault, on limestone hills near Montpellier. Several interesting aspects emerged: firstly, the abundance of *Glomeris* and *Cylindroiulus* populations was very high; secondly, the presence of *Polyzonium germanicum* was recorded, which was surprising for a species associated with waterlogged conditions near the centre of its west-European range (DAVID, 1990).

DAVID, J.-F., 1996. — The diplopod community of a mediterranean oak forest in Southern France: ecological and evolutionary interest. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 627-634. Paris ISBN : 2-85653-502-X.

As information on millipede communities in French Mediterranean forests remained scanty (BIGOT & BODOT, 1973; SAULNIER & ATHIAS-BINCHE, 1986; JANATI-IDRISSI, 1988), further investigations were carried out at Puechabon for two years. Results have been obtained on three points: (1) the seasonal changes in abundance have been described in terms of individuals and in biomass (DAVID, 1995), which will be summarized in the present paper; (2) the extraordinary abundance of macrosaprophagous species in the Mediterranean region has been confirmed; (3) some traits distinguishing the local populations from others of the same species have been underscored, as will be shown in *P. germanicum.*

SITE AND METHODS

The study site is located in the state forest of Puechabon, 25 km northwest of Montpellier, at an altitude of 260 m. The climate, though rather humid with a cool winter, is typically Mediterranean. Rainfall is minimal in summer, with a period of severe drought almost every year; the summer dryness index of EMBERGER (1943) is < 7. A red fersiallitic soil overlies karstic limestone; its clay content is high, as is the proportion of stones. The humus form is a mull, and measurements from nearby sites have given pH ≈ 7 and C/N ≈ 16 (FLORET *et al.*, 1989; MERZOUKI *et al.*, 1989). The forest is a holm oak coppice (*Quercus ilex*) with a typical understorey of shrubs and herbs made up of several tens of species (BRAUN-BLANQUET, 1936; DUGRAND, 1963).

Sampling was carried out in an area of about 3000 m^2 surrounding a cleared plot with a CNRS meteorological station. Eight samples, each including between 10 and 12 sampling units, were taken over two years: two in spring (30 April, 1991 and 1 May, 1992), two in early summer (5 June, 1991 and 23 June, 1992), two in early autumn (7 October, 1991 and 1 October, 1992) and two in winter (3 January, 1992 and 29 January, 1993). Each sampling unit consisted of two parts: (i) litter and soil down to about 2 cm deep, collected in a 25 x 25 cm quadrat (1/16 m^2); (ii) soil between 2 and 10 cm deep, collected with a cylindrical corer 10 cm in diameter (≈1/127 m^2). The largest millipedes were sorted by hand and the others extracted by Tullgren funnels in the laboratory. Species were determined according to DEMANGE (1981).

In order to assess the fresh biomass of Chilognatha, as many individuals as possible were weighed alive after cleaning on moist filter paper, then their species, sex and stadium were determined. For dead animals, the mean live mass corresponding to their species, sex and stadium was used.

The differences in abundance were compared statistically by means of parametric (STUDENT's t-test) and non-parametric (MANN-WHITNEY U-test) methods. The differences were considered significant if both tests gave a probability $P < 0.05$.

RESULTS AND DISCUSSION

The millipede species

A total of seven specifes were found at Puechabon. Four were present in all the samples: *Glomeris marginata* (Villers), *Cylindroiulus caeruleocinctus* (Wood), *Polyzonium germanicum* Brandt and *Polyxenus lagurus*[1] Linné. Another, *Opisthocheiron elegans* Ribaut, was present in seven out of eight samples. Two other species were found occasionally on the site: one specimen of *Ommatoiulus rutilans* (C. L. Koch) was collected in the samples and several others by hand, which made it possible to determine an adult male; two specimens of *Polydesmus* sp. were collected by hand.

JANATI-IDRISSI (1988) reported the presence of *Cylindroiulus londinensis* (Leach), *Ommatoiulus sabulosus* (Linné) and *Blaniulus guttulatus* (Fabr.), in addition to *G. marginata* and *P. germanicum*. In fact, *C. caeruleocinctus* was obviously mistaken for *C. londinensis*, as often happens in the literature, and there might also have been confusion of the two *Ommatoiulus* species. As for the blaniulid, it was not found during the present study.

Population density

Overall, the average number of millipedes and its standard-error, stadium I not included, was 667 ± 56 ind./m^2, 556 ± 55 of which belonged to Chilognatha and 111 ± 16 to Penicillata. The average biomass, for Chilognatha only, was 11.0 ± 1.1 g/m^2. From samples taken between

[1] Southern France is inhabited by the sexual form (NGUYEN DUY - JACQUEMIN, 1973).

1984 and 1986 and sorted by hand, which yielded the largest individuals, JANATI-IDRISSI (1988) had recorded a much lower number of Chilognatha (95 ind./m2 on average) but a barely lower biomass (2.8 g *dry mass*/m2, *i.e.* between 8 and 9 g/m2).

The seasonal population densities of the five main species are given in Table 1. For each season the data from the two years are pooled, as most differences between years were not significant. There were significant seasonal changes in the population density of two species: (i) the number of *G. marginata* was lower in spring than in early summer ($P < 0.05$) and early autumn ($P < 0.01$); likewise, its biomass was lower in spring than in early autumn ($P < 0.01$ for t-test; $P < 0.05$ for U-test); (ii) the number of *P. lagurus* was lower in early autumn than in early summer ($P < 0.01$) and winter ($P < 0.05$). In all other species, the seasonal variations in numbers of individuals and in biomass were not significant.

TABLE 1. — Seasonal abundance of the main millipede species at Puechabon (after DAVID, 1995). The results are in number and biomass / m2 ± standard-error. (s.u.: sampling units).

		SPRING (21 s.u.)	EARLY SUMMER (22 s.u.)	EARLY AUTUMN (22 s.u.)	WINTER (24 s.u.)	MEAN
G. marginata	Ind./m2	100 ± 16	216 ± 44	297 ± 47	228 ± 47	212 ± 22
	g/m2	4.0 ± 0.7	7.3 ± 1.6	11.5 ± 2.1	8.0 ± 2.2	7.8 ± 0.9
C. caeruleocinctus	Ind./m2	50 ± 11	124 ± 88	54 ± 11	38 ± 12	66 ± 22
	g/m2	3.3 ± 1.0	2.2 ± 1.3	3.1 ± 0.8	2.4 ± 0.9	2.7 ± 0.5
P. germanicum	Ind./m2	352 ± 124	311 ± 118	161 ± 62	247 ± 63	267 ± 47
	g/m2	0.4 ± 0.1	0.7 ± 0.2	0.4 ± 0.2	0.4 ± 0.1	0.5 ± 0.1
O. elegans	Ind./m2	21 ± 14	16 ± 10	1 ± 1	6 ± 3	11 ± 4
	g/m2	ε	ε	ε	ε	ε
P. lagurus	Ind./m2	119 ± 37	164 ± 37	42 ± 13	121 ± 30	111 ± 16
Total Diplopoda	Ind./m2	643 ± 132	831 ± 142	556 ± 76	640 ± 86	667 ± 56
Total Chilognatha	g/m2	7.8 ± 1.2	10.3 ± 2.4	15.0 ± 2.4	10.8 ± 2.5	11.0 ± 1.1

Aspects of the seasonal dynamics

Seasonal variations in population density are not easily explained, for they depend on both actual changes in abundance (*e.g.* recruitment; mortality) and apparent changes (*e.g.* burrowing into the deep soil). Both are considered in the following discussion — keeping in mind that the seasonal changes in the vertical distribution of species were measured in the daytime, and without data regarding the height of summer. The five most abundant species all exhibit different patterns.

G. marginata generally lives near to the surface, except in winter when it tends to go deeper (Fig. 1). The vertical distribution seems the same as in Great Britain, on the opposite side of its range (BOCOCK & HEATH, 1967). Recruitment occurs during warm months, as shown by the high number of stadium II individuals (8 tergites; 8 leg pairs) in the samples from early summer and early autumn. The species seems to withstand the summer drought easily, since there is a continuous increase in abundance from spring to autumn, both in number and in biomass (Table 1). On the other hand, *G. marginata* has difficulty in coping with winter cold;

while moving down in the soil, it undergoes a fall in abundance, which becomes minimal in spring (Table 1).

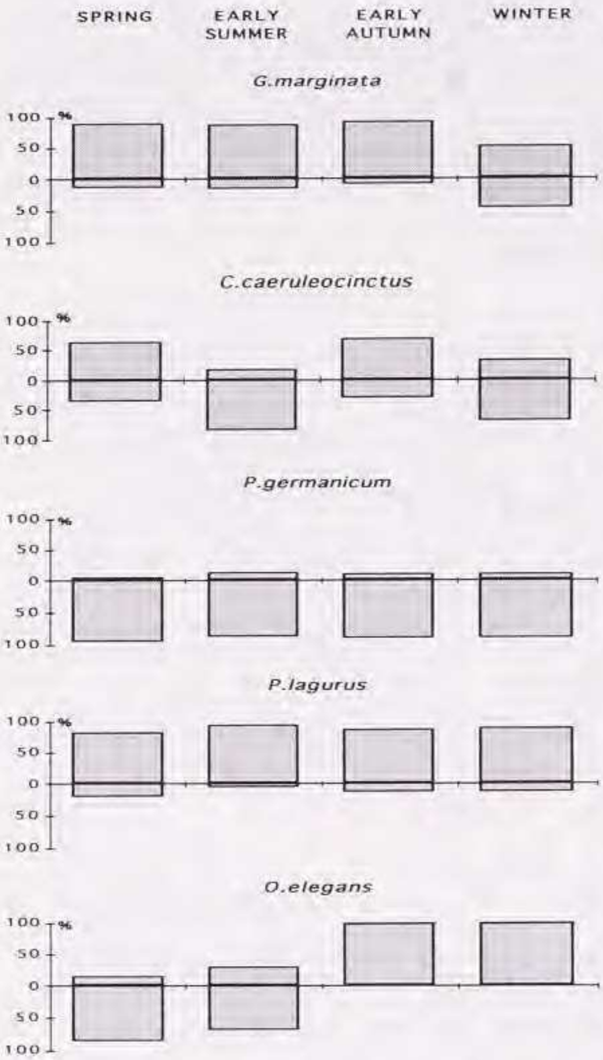

FIG. 1. — Seasonal changes in the vertical distribution of the main millipede species at Puechabon. The results are expressed as percentages of the population density (ind./m2) in two soil layers: (i) litter and top-soil down to 2 cm (above the line); (ii) soil between 2 and 10 cm deep (under the line).

C. caeruleocinctus appears to live a little deeper than *G. marginata* in spring and autumn but, like many julids in the temperate zone, it burrows markedly during summer and winter (Fig. 1). A batch of the smallest individuals (stadium IV; 3 rows of ocelli) were found in one sampling unit from the early summer of 1991, between 2 and 10 cm in depth, which may be indicative of the recruitment period. But if the young stay in the deep soil, that may explain why significant seasonal changes in density are difficult to detect.

P. germanicum is the most subterranean species at Puechabon (Fig. 1). Contrary to what could be assumed on the basis of Table 1, recruitment does not start in winter, but in summer; many brooding females were observed in spring, and stadium I individuals in early summer. But again, seasonal changes in density are difficult to detect because the whole cycle appears to occur deep in the soil; moreover, the spatial distribution is highly contagious (the variance to mean ratio reaches a maximum in this species).

In contrast, *P. lagurus* appears to remain in the litter and upper soil layer throughout the year (Fig. 1). The species seems sensitive to summer drought for its population density is significantly reduced in early autumn (Table 1). The subsequent increase during winter is suggestive of recruitment in the course of autumn, but the samples were not frequent enough to follow this fast-developing species.

The population density of *O. elegans* is low and the proportions given in Figure 1 are quite uncertain. Nevertheless, the species appears to live in the soil in spring and early summer, then to move upwards in autumn and winter (Fig. 1). These vertical displacements are concomitant with different stages in the life cycle, which looks annual at Puechabon (Table 2). Adults emerge by early autumn at the surface; they breed in winter, as shown by the appearance of the young of stadium II in January, still at the surface; then growth occurs deeper in the soil during drier months.

Ecological importance of saprophagous species

It is interesting to compare the abundance of macrosaprophagous millipedes — those which fragment litter for feeding, *i.e.*, mainly Glomerida, Julida and Polydesmida — in forests of different climatic regions of Europe. In the Atlantic zone, the density of these species is very variable, but peak biomasses are usually below 4 g/m2. The highest figures of fresh biomass recorded in Great Britain and northern France are, respectively, 3.9 g/m2 in autumn samples from a mixed mull-like moder (BLOWER, 1979) and 2.3 g/m2 in spring and autumn samples from an oak mull (DAVID, 1989). The figure of 7.5 g/m2 in a Danish beech mull provided by BORNEBUSCH (1930) may be an overestimate, owing to the approximate value of individual biomasses. Similarly, the highest biomass figure recorded in more continental regions of western Europe is an annual mean of 4 g/m2 for all Diplopoda, in a mixed oak wood in Austria (MEYER *et al.*, 1984).

Although data are more scarce in European regions of the Mediterranean, they are also very variable. Nevertheless, peak biomasses are higher than in the Atlantic zone, notably in climatic transition areas. IATROU (1989) has measured a density of 114 ind./m2 for macrosaprophagous millipedes in a community of northern Greece where *Glomeris balcanica* is dominant, which should correspond to a substantial biomass (above 7.1 g/m2, the figure for *G. balcanica* alone). The biomass of macrosaprophagous species at Puechabon is higher than all those mentioned above, on average 10.5 g/m2 for Glomerida and Julida.

Provided that the ingestion rate is of the same order of magnitude as in the conditions prevailing in the Atlantic zone (about 10 g dry litter/g fresh mass/year — (VAN DER DRIFT, 1975; DAVID, 1987), millipedes probably play a very important role in Mediterranean forest ecosystems. So it should be very interesting to pursue the ecological studies which have been undertaken on litter consumption by millipedes in that region (BERTRAND *et al.*, 1987; JANATI-IDRISSI, 1988).

TABLE 2. — Seasonal changes in the stadial composition of *O. elegans* at Puechabon (ind./m2). From stadium II in winter, individuals proceed to the adult stage in autumn, through stadium V in spring and stadium VII in early summer.

	STADIUM (and number of rings)							
	II (5/2)	III (7/3)	IV (10/4)	V (14/4)	VI (18/4)	VII (22/3)	VIII (25/2)	AD (27/2)
WINTER	3	1	1					1
SPRING			6	15				
EARLY SUMMER			ε		1	14	1	
EARLY AUTUMN								1

Particularity of local populations

From the taxonomic point of view, the millipede community of Puechabon does not differ from typical atlantic communities, since all the species present can be found further north. This similarity is misleading, however, for conspecific populations can be very different between the two areas. For example, if the *P. germanicum* population from the forest of Puechabon is compared with a population from the forest of Orléans, in the Centre of France, substantial differences emerge as regards colour and body size: (1) individuals from Puechabon are of paler yellowish colour than those from the forest of Orléans; (2) the difference in body size is striking, which can be shown by comparing the fresh weight of individuals in relation to their number of rings (Fig. 2); in both sexes, individuals from Puechabon are much smaller, the number of rings being equal.

Such intraspecific differences can be explained in two ways. Either there has been selection for different genotypes in the two populations, which would be closely adapted to local conditions, or there is phenotypic plasticity within the species for traits like colour and body size, in which case individuals from the two populations maintained in the same conditions would give the same phenotypes. Only cultures under controlled conditions could help to distinguish the correct explanation.

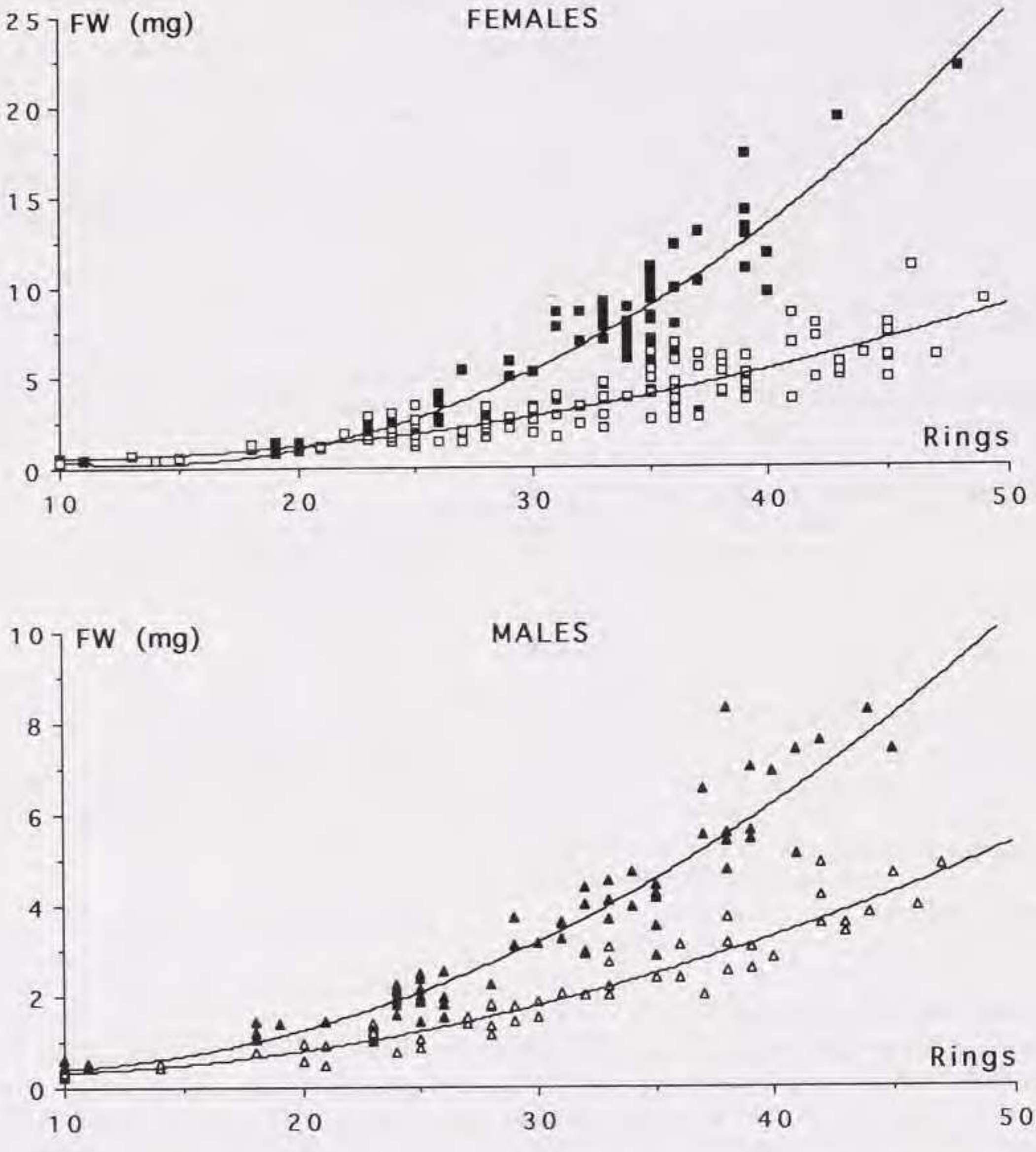

FIG. 2. — Comparison of the curvilinear regressions between fresh mass (FW) and number of podous rings, in *P. germanicum* populations from the forests of Orléans (black) and Puechabon (white). Individuals were collected from October to May on both sites.

However, the special selective forces that act at the periphery of a species range, in ecologically marginal areas, generally favour genetic differentiation of populations, regarding many morphological, physiological, behavioural or demographic traits (MAYR, 1963). As all the species present at Puechabon but *P. lagurus* are near the driest boundary of their geographical range (MAURIÈS, 1964; MAURIES & GEOFFROY, 1982; KIME, 1990a, b), it is tempting to suggest that such a genetic differentiation has occurred. This is a very likely scenario in the case of *P. germanicum*, which is probably a small isolate at Puechabon given the species' rarity in the Montpellier region.

Irrespective of the process actually involved, different factors can exert an influence on soil animals in Mediterranean areas (DI CASTRI, 1973). On one hand, the effects of climatic factors such as summer drought can be felt in species remaining near the surface of the soil. On the other hand, constraints associated with an endogeic way of life (*e.g.* low availability of resources) may be the driving force in species which avoid the severity of climate by their burrowing behaviour. As regards *P. germanicum*, its living in the soil in the Mediterranean forest (Fig. 1) contrasts strongly with its high abundance in the litter in the forest of Orléans (DAVID & COURET, 1985). Therefore, the differences in body size and colour between the two populations — whether they are genetic adaptation or phenotypic characteristics due to acclimatory or developmental responses — may result from their living in microhabitats differing in depth rather than in climate.

ACKNOWLEDGEMENTS

I am grateful to Prof. J.-P. LUMARET (University of Montpellier III) for information on the study site; to J.-J. GEOFFROY and J.-P. MAURIÈS (MNHN, Brunoy and Paris) for the identification of some specimens; to M. GRANDJANNY and F. ROMANE (CEFE-CNRS, Montpellier) for providing local climatic data; and to H. READ for improvements in English.

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